# Translocation of Threatened Tiger Beetle Cicindela dorsalis dorsalis (Coleoptera: Cicindelidae) to Sandy Hook, New Jersey

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ABSTRACT The two key objectives of the recovery plan for the Federally threatened tiger beetle Cicindela dorsalis dorsalis Say are to protect populations within the Chesapeake Bay and to establish by reintroductions new populations in the U.S. northeast (New Jersey to Massachusetts). This article reports on the development and implementation of translocation work to establish a population of C. d. dorsalis at Gateway National Recreation Area, Sandy Hook, NJ, by using larvae from Chesapeake Bay populations. Previous experimental translocation trials in Virginia by using adults were unsuccessful because the adults dispersed from the translocation sites within 1-2 wk. Experimental translocations were conducted to test methods with larvae from several Virginia sites to Sandy Hook in September 1994 and 1995. The translocated larvae readily dug burrows, many survived the winter, and some emerged as adults the following summer. Additional translocations of >475 larvae each year were conducted in early May 1997, 1999, and 2000. Peak numbers of emerging adults counted each year in Tuly increased from 178 in 1997 to 749 in 2001. Adults exhibited normal behaviors in the field (foraging, thermoregulation, and mating) and recruited larvae each year. A population seemed to be successfully established, but adult numbers declined sharply after the 2001 peak to 142 in 2002, 43 in 2003, and six in 2004. We have little evidence for the cause of this sharp decline in adult numbers, but it may have resulted from predation by gulls, dispersal triggered by the high gull densities where beetles occurred, or perhaps from coastal storm impacts causing a progressive decline in survival and recruitment of the beetle population. The initial success of this translocation suggests that efforts using these methods should be continued, but closer monitoring at the translocation site is needed to determine the fate of the population. These methods also may be applicable to the recovery of other threatened or endangered tiger beetles.

KEY WORDS Cicindelidae, tiger beetle, translocation, recovery

THE ESTABLISHMENT OF NEW populations by reintroductions with captive-reared individuals or those from existing populations has been an effective approach for the recovery of many endangered and threatened species. The successful recovery work with translocations of the gray wolf, Canis lupis L.; California condor, Gymnogyps californianus Shaw; and other vertebrates is well known, but reintroductions of insects are much less common, despite insects being more easily reared and translocated than vertebrates. Probably the most successful recovery work with an insect has been with the Schaus swallowtail, Papilio aristodemus ponceanus Schaus. Captive rearing and restoration of habitat (planting of larval host plants and adult nectar plants) at potential translocation sites has greatly improved the status of this species (Daniels and Emmel 2004). Reintroductions using captive reared individuals also have been used in the recovery

efforts with the butterfly Glaucopsyche lygdamus palosverdesensis Perkins & Emmel (Gross 1997) and the beetle Nicrophorus americanus Olivier (Amaral et al. 1997).

The tiger beetle Cicindela dorsalis dorsalis Say was listed by the U.S. Fish and Wildlife Service as a threatened species because of its widespread extirpation in the U.S. northeast (New Jersey to Massachusetts) and threats to existing populations within the Chesapeake Bay (USFWS 1990). Before the 1940s C. d. dorsalis was widespread and abundant on sandy beaches along the Atlantic coast from Cape Cod to central New Jersey and at a few locations along the Chesapeake Bay shoreline (Knisley et al. 1987). It was so abundant that Leng (1902) reported it "occurring in great swarms during July." The Atlantic coast populations experienced widespread extirpation from 1900 to 1950 because of the increasing heavy recreational activity and development of the sandy beach habitats. The beetle was believed to be extirpated in the northeast until a population was found on Martha's Vineyard in 1990 (USFWS 1993). Subsequently, two other small popu-

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lations were found, one nearby at Martha's Vineyard and another on the mainland of the southern Massachusetts coast. Surveys of the whole Chesapeake Bay shoreline conducted since the listing have reported *C. d. dorsalis* at nearly 100 sites, but many sites have only small populations or are threatened by shoreline development and modifications (Knisley and Schultz 1997).

The two primary objectives included in the recovery plan for *C. d. dorsalis* were to 1) protect at least 26 existing Chesapeake Bay populations and 2) reintroduce populations to sites within the historic range of *C. d. dorsalis* in the northeast (USFWS 1993). Considerable progress has been made in the protection of Chesapeake Bay populations, with 14 sites in Virginia and Maryland now having some level of protection. The reintroduction part of the recovery plan is more challenging because few suitable (protected, undisturbed) sites are available in the northeast and a successful reintroduction protocol did not exist. In this article, we describe the development of a translocation procedure and the results of trial implementation of the plan.

#### Materials and Methods

Previous attempts at developing translocation methods for C. d. dorsalis used adult beetles. Two translocation trials involved moving 50-100 adults from sites in Virginia to other nearby beach sites that had similar habitat but few or no adults (Knisley and Hill 1991, Hill and Knisley 1994). The adults were collected at one site, each marked by scratching off pronotal setae and then released at the translocation site. The sites were resurveyed to count adults at 2- to 5-d intervals for several weeks. Another trial translocation in Massachusetts involved moving 50 adults from the Martha's Vineyard population to a historic site on Cape Cod from which the species was extirpated in the 1940s (P. Nothnagle, unpublished data). The adults were counted every few days for several weeks. In each of these trials, nearly all of the adults dispersed from the translocation sites within 1-2 wk. Adult tiger beetles, including C. d. dorsalis, are known to commonly disperse, often great distances, but the factors that trigger these movements are unknown (Knisley and Schultz 1997).

The results with adults and previous studies of moving tiger beetle larvae (C.B.K., unpublished data), suggested that translocation of larvae may have a greater chance for success. We had observed that larvae of several species of tiger beetle would readily dig new burrows and continue developing when moved to new locations in the field or in the laboratory. Discussions with members of the *C. d. dorsalis* Recovery Group resulted in the development of the plan, described herein, to establish a population at Gateway National Recreation Area, Sandy Hook Unit, NJ. The plan was to first conduct "experimental" translocations to test the methods of larval translocation, and if these were successful, proceed with multiple, larger scale translocations. Described below are the

methods and results for two experimental translocations (in 1994 and 1995) and three primary translocations (in 1997, 1998, and 2000).

Source Sites and Translocation Site. Our requirements for a suitable translocation site were that it be a known or probable historic site in New Jersey and that it have limited human disturbances. Specifically, suitable sites would have little pedestrian foot traffic and no vehicle activity. Very few sites met these criteria because most were recreational beaches with high levels of human activity. The most promising site selected was the northern end of Gateway National Recreation Area, Sandy Hook, NJ. The last specimens of C. d. dorsalis were collected there in 1940, but our surveys of this site in 1985 and 1993 indicated that the population had been extirpated. Two adjacent beaches at Gateway (North Beach and Gunnison Beach) were selected. Both had relatively low levels of human use because they were away from beach access points and were closed to the public from April through September to protect piping plovers, Charadrius melodus Ord, also a federally listed species. This time of restricted beach use was also a critical time for protecting C. d. dorsalis because larvae are active primarily in late spring and fall and adults emerge, mate, and oviposit during July and August.

Source Populations. The decision to use beetles from the Chesapeake Bay for translocation was made with some reservations because mitochondrial DNA studies indicated that Massachusetts *C. d. dorsalis* and possibly those in New York and New Jersey were genetically different from those at Chesapeake Bay sites (Vogler and DeSalle 1993). However, the largest New England population was too small to sustain the removal of several hundred larvae for translocation and unlikely to ever yield enough material for large-scale translocations.

The five Chesapeake Bay sites selected for providing larvae (75-150 from each site) were in Northumberland County, Virginia, and had consistently large populations (all with >1,500 adults). Two methods were used for collecting larvae from these sites. The most efficient method was to search for larvae at night by using a hand-held spotlight. When larvae were found at the top of their burrows, a hand trowel taped to the end of a 1.5 m long pole was rapidly inserted under the burrow to trap the larvae at the surface. When larvae were not active at night we dug them from their burrows the next day. A grass stem was placed into the larval burrow and the sand was then carefully removed from one side of the burrow along the stem until the larvae were located. Each larva that we collected was placed in a separate wide-mouth 30-ml plastic vial with damp sand. In the field, the vials were placed in a cooler with ice; then later, in the laboratory, they were transferred to a low-temperature incubator at 5°C for 1-2 d until a sufficient number of larvae had been collected. The vials with larvae were then placed in several large coolers with ice and taken to the translocation site at Sandy Hook where they were placed the same day.

Table 1. Numbers of larvae translocated, emerged adults, and larval progeny in translocations at Gateway National Recreation Area, New Jersey

	Translocation site	Translocated larvae				77 . 1 3 1.	
		First	Second	Third	Total	Emerged adults	Larval progeny
Experimental Translocation 1994	North Beach	6	202	192	400	48*	20*
Experimental Translocation 1994	Gunnison	55	111	132	298	7*	0*
Experimental Translocation 1995	North Beach	159	10	2	171	18**	3**
Experimental Translocation 1995	Gunnison	118	4	2	124	1**	0**
Primary Translocation 1997	North Beach	0	28	458	484	178	22
Adult Counts 1998	North Beach					48	n.s.
Primary Translocation 1999	North Beach	0	28	557	585	260	13
Primary Translocation 2000	North Beach	0	48	506	554	720	21
Adult Counts 2001	North Beach					749	46
Adult Counts 2002	North Beach					142	n.s.
Adult Counts 2003	North Beach					50 -	n.s.
Adult Counts 2004	North Beach					6	n.s.
Total					1,623	2,153	n.s.

<sup>\*, 1995</sup> counts; \*\*, 1996 counts; n.s., no survey.

At the translocation site, all translocated larvae were placed along a 150-m long by 40-m wide section of beach that was located 3-5 m above the current high tide line. Two different patterns of larval placement were used. In the two experimental translocations, vials with larvae were set out in 10 by 20-m plots with 10 rows of 20 larvae each. Each larva was thus 1 m from adjacent larvae. We used this arrangement so we could easily monitor them later to determine survival and activity.

In the three primary translocations, we did not monitor larvae after placement so we used a different arrangement but in the same 150-m section of the beach. The vials were placed onto the sand in 16–20 separate 2 by 10-m patches, each patch 30–60 m apart. One-half of the patches were placed 3–5 m above the high tide line, and the other half were located 20–40 m further back on the beach. The vial placement within each patch consisted of two rows (1 m apart) with 15 vials (6–7 cm apart).

Because tiger beetle larvae do not readily dig burrows in dry sand, we used a sprinkling can with ocean water to wet the sand within each row or patch to a depth of 8–15 cm before releasing the larvae. The larvae were then emptied from the vials onto the sand surface and confined by pressing the vial into the damp sand. Most larvae began digging burrows within 5–15 min. The vials were collected after 60–90 min when nearly all of the larvae, except a few that were injured or inactive, had dug burrows. The translocated larvae were rechecked the next day, and the total number that had established burrows was counted.

Placement of larvae in the two experimental translocations in late September 1994 and 1995 were at two adjacent beaches along the northernmost shoreline at Gateway National Recreation Area (Table 1). In 1994, we released primarily second and third instars, 400 at North Beach and 298 at Gunnison Beach. In the 1995 translocation we released mostly first instars, 219 at North Beach and 148 at Gunnison Beach. The three primary translocations were carried out in late April to early May 1997, 1999, and 2000 with the objective of establishing a population at Sandy Hook. Each of these

translocations included >475 larvae, mostly third instars (Table 1). Only North Beach was used for the latter three translocations because the experimental translocations indicated better survivorship and emergence.

By using primarily third instars and translocating them in late spring, we intended to reduce the length of time larvae spent at site and thus increase rates of survival and emergence. We expected that many of the third instars were mature enough to pupate at Sandy Hook soon after translocation, emerge as adults in July, and ideally begin recruitment of a larval cohort that might develop into new adults in 2 yr (the probable life cycle of this species in New Jersey).

Monitoring of larvae in the experimental translocations was conducted 2, 4, and 6 wk after translocation to determine the numbers that were active (indicated by open burrows) and to record any movement (indicated by open burrows beyond the placement locations) by the larvae. We did not monitor larvae in the three primary spring translocations because we expected they would quickly plug their burrows in preparation for pupation.

Surveys to determine numbers and distribution of emerging adults were conducted on two or more dates every year from 1995 to 2004. The first survey each year was on 2-15 July (on warm sunny days) when we expected most of the adults would have emerged and be near peak abundance. A second count was made from 17 to 25 July to determine whether adult numbers were declining. In some years, an August check of adult numbers also was done. The counts were made by two or more workers walking slowly along the shoreline, one along the wet edge and the others along the adjacent middle beach, each counting all adults seen within a 15-20-m-wide band. The survey area was ≈1,800 m in length, extending from the far north end of Sandy Hook (≈400 m north of North Beach) to ≈150 m south of the Gunnison Beach (600 m south of North Beach). In addition to counting adults, we also recorded observations of adult activities (e.g., foraging and mating). In September to mid-October of each year, we did one or two surveys to

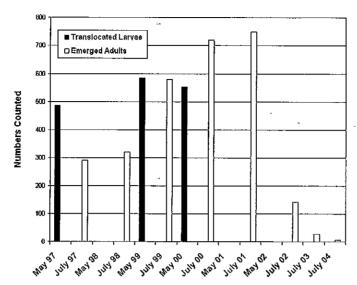


Fig. 1. Numbers of translocated larvae and emerging adults in two experimental and three primary translocations at Gateway National Recreation Area, NJ, 1994–2004.

count the burrows of any new larvae that might have developed from ovipositing adults. These surveys involved 3–4 h visual searches within a 5-m-wide by 200-m-long section of the berm area of the beach where adults were most abundant during summer surveys and where larvae were most likely to occur.

### Results

The monitoring of larval activity in the weeks after the two fall experimental translocations indicated only a small percentage of larvae were active. In the 1994 translocation, 125 (67 at Gunnison Beach, 68 at North Beach) of the 698 larvae (18%) were active 2 wk after translocation, and 33 (5%) were active after 4 wk. Four of the first instars progressed to the second instar during this period. Only 14 active larvae were found the following April.

In the second experimental translocation, 34 of 336 larvae monitored (9%) were active after 2 wk, 48 (14%) after 4 wk (25 at Gunnison Beach, 23 at North Beach), and nine (3%) after 6 wk. During this period, three first instars progressed to second instars and one second progressed to a third instar. In both years, we found small numbers of disturbed larval burrows where larvae were possibly killed by ghost crabs. Surveys of adults that emerged from the successful development of the translocated larvae produced peak counts of 48 adults in early July 1995 and 18 in July 1996 (Table 1). Additional evidence for potential success of the experimental translocations was our observation of normal behavior of emerged adults (mating, foraging, and thermoregulating) and the presence of small numbers of new C. d. dorsalis larvae in September 1995 (18 first instars, 2 second instars) and 1996 (one first instar, 2 second instars).

The three primary translocations (1997, 1999, and 2000) resulted in large and increasing numbers of

emerging adults: 178 in 1997, 260 in 1999, 720 in 2000, and 749 in 2001 (Fig. 1) during the early July surveys. Adult numbers were lower each year in the late July to mid-August counts. The low count of 48 adults in 1998 was in a year in which there was no translocation. Nearly all of the adults in each of the surveys were found within a 200-300-m section of shoreline centered near the area where the translocated larvae were placed. In the early July surveys in 2000 and 2001, densities in this area were commonly 10-20 adults per 20-m length of beach. Densities decreased north and south of this area, but a few adults (4-10 individuals) were found as far as 500 m north and 150 m south of this primary concentration. Observations during the surveys indicated that the adult beetles were feeding, mating, and exhibiting behaviors characteristic of the species. After the high count in 2001, adult numbers declined dramatically to 142 in 2002, 43 in 2003, and six in 2004 (Fig. 1).

Early instars that resulted from successful mating and oviposition by emerging adults were found each year in the late summer—early fall surveys. The numbers of larvae counted were 22 (four first instars, 18 second instars) in 1997, 13 (four second instars, nine third instars) in 1999, and 33 (seven first instars, 14 second instars, and 12 third instars) in 2000. No larval surveys were conducted in 1998 or after 2000.

#### Discussion

The results of this study suggest that new populations of *C. d. dorsalis* may be successfully established by using the larval translocation methods described in this study. The previous trials with adults were not successful because adults quickly dispersed from the translocation sites. Our results with adults are in contrast to those of Brust (2002) who was able to establish a small population of *C. formosa* in a patch of sand dune

by translocating adults. The different results may reflect a difference among species or in the types of habitats involved. In our trials with *C. dorsalis*, there was additional beach habitat adjacent to the translocation sites, whereas in Brust's study the small sand dune was surrounded by unsuitable habitat.

The most important indicators of the success of our larval translocations were the large and increasing numbers of adults at Sandy Hook after translocations (1999–2001), the recruitment of new larvae by these emerging adults, and the apparent development of some individuals through their complete 2-yr life cycle at Sandy Hook. The best evidence for production of new individuals at the site was the 720 adults counted in 2001, a year after translocations. Some of these were from larvae translocated in 2000 that had slower development and did not emerge until 2001, but others were apparently individuals that developed from eggs laid by the 1999 adults. Other studies with *C. dorsalis* suggested this species requires 2 yr for development in most of its range (Knisley and Schultz 1997).

Additional evidence of the translocation success is that the combined total of emerging adults from 1998 to 2004 was greater (2,153) than the total numbers of larvae translocated (1,625). It is also likely that the actual numbers of adults at Sandy Hook were probably greater than indicated by our index count. Previous studies with C. d. dorsalis and several other tiger beetles species indicated that the visual index counts greatly underestimate actual numbers present (Knisley and Schultz 1997). We are uncertain why only a small percentage of the larvae were inactive after the two experimental translocations, but the disturbance of moving them could have triggered prolonged burrow plugging and inactivity. Many of the larvae also may have plugged their burrows in preparation for overwintering, which typically occurs in mid- to late October. Our fall surveys for larvae recruited by the emerging adults produced relatively small numbers, but this is not unusual because we were able to survey only a small portion of the wide zone of potential habitat available at the translocation site.

The cause of the sharp decline in numbers of C. dorsalis adults at Sandy Hook from 2001 to 2004 is unknown, but anecdotal information suggests it could have been due to predation by gulls. During previous years (1996-2000) when we did adult beetle counts, we observed moderate numbers of gulls (50-75 individuals) along the several hundred-meter section of beach where most adult beetles were concentrated. Most were identified as laughing gull, Laurs atricilla L.; lesser black-backed gull, Larus fuscus L.; and herring gull, Larus argentatus Pontoppidan. However, during the 2002 counts on both dates in July, the numbers of birds increased to an estimated 700-1000 in the same beach area where most beetles were. Adult C. dorsalis numbers in 2002 declined from 142 on 2 July to 13 on 17 July. In previous years, adult numbers did not decline to this extent until very late July to early August. For example, in 2000 the count was 720 adults on 10 July, 678 on 17 July, and 188 on 25 July. We speculate that many of the emerging adults were quickly preved

upon by these gulls before our 2 July count and most of those surviving until 2 July were then taken before the 17 July count.

We did not directly observe feeding by gulls on tiger beetles, but there are reports of significant predation by gulls and other shorebirds on tiger beetles (Larochelle 1975). Most relevant was the report by Greenhalgh (1952) who found 538 unidentified tiger beetles in 42 California gull, Larus californicus Lawrence, stomachs in Utah. Adult tiger beetles foraging or mating along the water edge would be exposed to resting gulls and be easy prey. The gull density was so high that most of the beach surface in this area was within a meter of a gull. Alternatively, the presence of gulls at such a high density may have been so disruptive to adult beetles that it caused beetles to disperse from the area. However in 2002, as in surveys in previous years, few beetles were found along the shoreline north and south of North Beach.

Our explanation of gulls as a cause of the decline of adult C. d. dorsalis is speculative, and other factors may be more important. Populations of tiger beetles, including those of C. d. dorsalis, are known to experience dramatic year-to-year fluctuations in abundance. often as a result of climatic factors or human-related habitat alterations (Knisley and Schultz 1997, Knisley et al. 1998, Knisley and Hill 2001). The progressive decline in adult numbers from 2001 to 2004 could have been a result of such factors causing winter mortality, low recruitment, and subsequent decline in adult numbers. The North Beach site at Sandy Hook is very dynamic and subject to significant impacts from coastal storms. Because the larvae of C, d, dorsalis spend 2 yr in this dynamic habitat during their development, some or all of the population would have a high probability of being negatively impacted by storms.

The results of this work validated, at least in part, our plan of translocating Chesapeake Bay beetles to northern New Jersey. The recovery group voiced reservations not only because of the genetic differences (Vogler and DeSalle 1993) but also because the shoreline habitats of the two areas are very different. The Chesapeake Bay beaches where C. dorsalis occurs are typically only 3-10 m in width with an intertidal zone of 1-2 m. Beaches at Sandy Hook are 20 to >40 m wide in most areas with an intertidal zone of 5-10 m. Sandy Hook, and other northeastern beaches are also subject to significant width reduction during late fall and winter whereas in the Chesapeake Bay there is very little seasonal change. Consequently, adults that oviposit in the upper intertidal zone and larvae that spend the winter on the upper beach must be adaptable to these different conditions.

The methods we describe here should be applicable to recovery of other federally listed tiger beetles, including *C. puritana*, *C. ohlone*, and *C. nevadica lincolniana*. For these species, however, laboratory rearing of larvae from field-collected adults may be necessary because of the small number and size of existing populations. Getting field-collected adults to oviposit and rearing the larvae to second or third

instars is possible and has been done for a variety of species (Knisley and Pearson 1984, Knisley and Schultz 1997). These methods would have to be scaled up to produce the larger numbers of larvae needed for effective translocations. The numbers of larvae needed to effectively establish a population is unknown and may vary with the biology and habitat of the species involved. For C. d. dorsalis, we had a number of very large populations available and could easily translocate large numbers of larvae, but it is possible that smaller numbers may have achieved favorable results. For species such as C. ohlone that occur in smaller patches of less dynamic habitat, fewer larvae (perhaps ≤100) may be effective in establishing a population. The number of populations that need to be established or present in an area is also an important consideration for recovery of rare species. Many species of tiger beetles exist as metapopulations and depend on dispersal and interchange among individual populations for long-term survival (Knisley et al. 1987, Pearson and Vogler 2001, Daniels and Emmel 2004), so multiple populations within dispersal range of the species may be needed to sustain individual populations and/or the species. It is possible that the lack of other nearby populations contributed to the decline of the C. dorsalis population at Sandy Hook.

In summary, we recommend that further efforts to recover the Northeastern beach tiger beetle by using larval translocations be continued. Closer monitoring at the translocation sites is necessary so that habitat changes or other factors that might impact the beetle population can be better understood.

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#### References Cited

Amaral, M., A. Kozol, and T. French. 1997. Conservation status and reintroduction of the endangered American burying beetle. Northeast. Nat. 4: 121–132.

- Brust, M. L. 2002. Reintroduction study on Cicindela formosa generosa in Marinette County, Wisconsin. Cicindela 34: 5-7.
- Daniels, J. C., and T. C. Emmel. 2004. Florida golf courses help save endangered butterfly. USGA Turfgrass Environ. Res. Outlook 3: 1-7.
- Greenhalgh, C. M. 1952. Food habits of the California gull in Utah. Condor 54: 302–308.
- Gross, G. 1997. Teaming up for PV blues. Endangered Species Bull. 22: 24-25.
- Hill, J. M., and C. B. Knisley. 1994. Experimental removal and reintroduction of the federally threatened tiger beetle Cicindela dorsalis dorsalis Say at a small beach habitat in Fleeton, VA—dispersal, site fidelity and mark-recapture. Unpublished report. U.S. Fish and Wildlife Service, Annapolis, MD.
- Knisley, C. B., and J. M. Hill. 1991. A trial reintroduction of Cicindela dorsalis dorsalis at two Chesapeake Bay sites. Unpublished report. Massachusetts Natural Heritage Program, Boston, MA.
- Knisley, C. B., and J. M. Hill. 2001. Biology and conservation of the coral pink sand dunes tiger beetle, Cicindela limbata albissima. West. N. Am. Nat. 61: 381-394.
- Knisley, C. B., and D. L. Pearson. 1984. Biosystematics of larval tiger beetles of the Sulphur Springs Valley, Arizona. Descriptions of species and a review of larval characters for Cicindela (Coleoptera: Cicindela). Trans. Am. Entomol. Soc. 110: 465–551.
- Knisley, C. B., and T. D. Schultz. 1997. The biology of tiger beetles and a guide to the species of the south Atlantic states. Virginia Museum of Natural History, Martinsville, VA.
- Knisley, C. B., J. I. Luebke, and D. R. Beatty. 1987. Natural history and population decline of the coastal tiger beetle *Cicindela dorsalis* Say (Cicindelidae: Cicindelidae). Va. J. Sci. 38: 293–303.
- Knisley, C. B., J. M. Hill, and C. A. Schulz. 1998. Distribution and abundance of *Cicindela dorsalis dorsalis*, the northeastern beach tiger beetle, along the western shoreline of the Chesapeake Bay in Virginia. Banisteria 12: 23–29.
- Larochelle, A. 1975. Birds as predators of tiger beetles. Cicindela 7: 1–7.
- Leng, C. W. 1902. American Coleoptera. Trans. Am. Entomol. Soc. 228: 95–185.
- Pearson, D. L., and A. P. Vogler. 2001. Tiger beetles: the evolution, ecology, and diversity of the cicindelids. Cornell University Press, Ithaca, NY
- [USFWS] U.S. Fish and Wildlife Service, 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Puritan tiger beetle and the Northeastern beach tiger beetle. Fed. Reg. 55: 32088-32094.
- [USFWS] U.S. Fish and Wildlife Service. 1993. Northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*) recovery plan. Hadley, MA.
- Vogler, A. P., and R. DeSalle. 1993. Phylogeographic patterns in coastal North American tiger beetles (*Cicindela dorsalis* Say) inferred from mitochondrial DNA sequences. Evolution 47: 1192–1202.

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